

A TAXONOMIC STUDY OF THE GENUS *PHYSALIS*  
IN NORTH AMERICA NORTH OF MEXICO<sup>1</sup>

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LINNAEUS founded the genus *Physalis* in 1753 with nine species, two of which are now usually referred to *Withania*. Five of the remaining seven are found within the area of the present study, although one, *P. Alkekengi*, is known only as a horticultural species, or as an escape from cultivation. In the second edition of *Species Plantarum* (1762) Linnaeus added two more species, *P. pensylvanica* and *P. peruviana*. The former does not occur in Pennsylvania and perhaps is not found in North America. In any event, it is considered to be a synonym of *P. viscosa*. *P. peruviana* is sometimes cultivated. Perhaps it escapes, but, if so, it is rarely collected. Pre-Linnean authors were familiar with the genus under the names *Physalis*, *Solanum* and *Alkekengi* as indicated in the Linnean references. Philip Miller (1768) described two species coming within the scope of this study. One of them, *P. virginiana*, is here interpreted as it has been for the last sixty years, although the application of the name is by no means certain.

Michaux (1803) described *P. lanceolata* and *P. obscura*, the latter consisting of var. *glabra* and var. *viscidopubescens*. Nees (1831) described *P. heterophylla*, *P. lanceifolia* and *P. Linkiana*.

*P. crassifolia*, the common species of southwestern desert regions, was described by Bentham (1844). Thomas Nuttall, in publications hereinafter enumerated under the species concerned,

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He is also thankful to the curators of several herbaria whose loans of all, or selected parts, of their valuable collections of *Physalis* made this study possible. They have loaned 8090 sheets of *Physalis* and related genera. Of this total, there are 5716 sheets of *Physalis* included in the present study. Many of the remainder were collections from other areas which materially aided in the formation of species concepts. These herbaria, listed by the standardized abbreviations published by Lanjouw and Stafleau (1954), are: ARIZ, COLO, DUKE, GH, KANU, LIL, MICH, MO, NY, OKL, OKLA, P, PH, RM, SMU, TEX, UARK, UC and WIS.

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described *P. angustifolia*, *P. longifolia*, *P. mollis*, *P. pumila* and *P. Walteri*. Dunal (1852) described *P. nyctaginea*, now generally referred to *P. heterophylla*.

In his study of the North American species, Asa Gray (1875) described *P. Fendleri*, *P. hederæfolia* and *P. Wrightii*. Rydberg (1896), in the last general study of the genus, described *P. ciliosa*, *P. comata*, *P. macrophysa*, *P. neomexicana*, *P. rotundata* and *P. versicolor*.

Following this, as a result of increased botanical activity, Mohr (1899) described *P. monticola*; *P. rigida* was described by Pollard and Ball (1900), and *P. polyphylla* by Greene (1900). *P. missouriensis* and *P. subglabrata* were proposed by Mackenzie and Bush (1902). Rydberg added *P. floridana*, *P. pendula* and *P. sinuata* in Small's Manual (1903). Aven Nelson (1909) proposed *Quincula lepidota* and *P. genucaulis*. *P. caudella*, described by Standley (1937) from Chihuahua has been found in southern Arizona, and these collections usually have been identified as *P. lanceolata*.

Margaret Y. Menzel (1951) has published an exploratory survey of the cytology and genetics of many of the species of our area, as they were interpreted by Rydberg, and various collectors who followed that author's treatment. Her work is valuable because it shows that the observed variation may indeed be correlated with cytologic and genetic differences.

#### TAXONOMIC CHARACTERISTICS

The stability of taxonomic characteristics apparently has been much disturbed by the long-continued distribution of various species by man as esculents. Some of the species, such as *P. ixocarpa* and *P. peruwiana*, are still so used. No doubt many of the species have been used by aborigines of many parts of the world at one time or another. This introduces the possibility of gene interchange between taxa that would otherwise not be contiguous. Furthermore, man's activities in producing disclimaxes provide habitats in which individual plants, or populations, of narrow ecological amplitude may survive. Such ecological niches might not have existed otherwise. It may be significant that many collections of *Physalis* are made in such disturbed habitats. Somewhat similar situations are admirably discussed by Edgar Anderson (1949).

The following discussion concerns the principal morphological characteristics which have been used in the taxonomy of the genus.

**ROOTS.** Both annual and perennial species occur in the genus. The former have fibrous root systems, or sometimes taproots. The latter are usually woody-based or rhizomatous. The annual vs. perennial characteristic has been used much in the past, beginning with Linneaus, to divide the genus into two main divisions. Since most herbarium specimens do not show the underground parts, this system is not a particularly convenient one. More dependence has been placed on other structures in the following treatment.

**STEMS.** All of our species have herbaceous stems, although in Mexico and Central America shrubby ones may occur. They may perennate from a woody caudex in such species as *P. crassifolia* of the desert areas of southwestern United States. Several of them grow from rhizomes, which may be cord-like, near the surface, and are often present in herbarium collections, as *P. arenicola* of sandy areas of Georgia and Florida, or thick, deeply buried and seldom collected, as the wide-ranging *P. heterophylla* and *P. virginiana*. The stems may be erect to prostrate and simple to much branched. An extreme in branching is found in *P. crassifolia* which, as reported by Jepson (1925), forms plants "1-3 ft. broad and  $\frac{1}{2}$ -1 ft. high."

**LEAVES.** The leaf blades are usually ovate to ovate-lanceolate, but they may be reniform, as are rarely some of the lower leaves of *P. hederæfolia*, or narrowly linear as in *P. angustifolia*. Petioles may be longer than the blade, or the blades may taper into short, winged petioles. The leaves are normally alternate, but sometimes appear to be opposite as in *P. viscosa* var. *Elliottii* which often has two leaves at a node, particularly in the upper part of the stem.

Leaf shape has often been used as a basis for establishing, or characterizing, taxa, as is indicated by such names as *latifolia*, *hederæfolia*, *angustifolia*, *heterophylla*, *lanceifolia*, *integrifolia*, *crassifolia*, *spathulaefolia* and *longifolia*. No doubt in some instances, as in *P. angustifolia* with its long linear leaves, the emphasis on leaf-form is justified. However, the size, shape and margins of leaves are extremely variable characteristics in groups that appear to be natural populations. One approach to the

understanding of this variability is to study a species that is well-delimited otherwise. An excellent example is *P. lobata*, a species so distinct that it has been considered a separate genus by such taxonomists as Rafinesque and Rydberg. Here the leaf shape may vary from narrowly ovate to linear-oblong, and the margins from pinnatifid to entire. Although the variation in leaf margins appears to be at an extreme here, the variability of leaf shape can be duplicated, and the variability in margins approached, in several other natural populations.

Under such conditions it would seem hazardous to establish species or varieties based on these characteristics; such a procedure should be followed only when these features are correlated with other morphological characteristics, or with geographic distribution. The author has utilized these criteria in maintaining *P. viscosa* var. *spathulaefolia* of the Texas gulf, and *P. viscosa* var. *maritima* of the southeastern seacoast. Here the extremes are distinct, but variation makes some collections difficult to place. Measurements of many specimens show the leaves of the former to be narrower than the latter, as indicated later in the keys to the species. However, if these features are used with the idea of either matching specimens, or describing new species, only confusion can result.

VESTITURE. The indument varies from hairs that are stellate or variously branched, to long jointed hairs and short hairs, capitate or sessile glands, or small crystalline vesicles as in *P. lobata*. Even the seemingly glabrous species usually have a few trichomes of some kind, at least on the younger parts. Frequently two or more kinds of trichomes are intermixed.

Such names as *viscosa*, *mollis*, *comata*, *pubescens*, *hirsuta*, *cinerascens*, *ciliosa*, *villosa*, *pruinosa* and *subglabrata* indicate the consideration that authors have given to indument in the past. The procedure seems to be partly justified. Surely the "stellate" populations are related. But if one attempts to distinguish taxa on the basis of the density or the size of the stellate hairs, caution should be exercised. In this study *P. viscosa* var. *mollis* has been segregated from var. *cinerascens* partly by this characteristic, but the latter taxon is extremely variable within itself in this respect. In *P. heterophylla* many of the variations in vestiture seem to be so little correlated, either with other characteristics, or with

geographic distribution, as to be unusable to distinguish even varieties. On the other hand, in *P. virginiana*, *sens. lat.*, the correlations are such that they are of value in helping to establish geographic varieties. In the *P. angulata*-*P. pubescens* series indument is also of taxonomic significance, the villous *P. pubescens* usually having abundant multi-cellular hairs, *P. angulata* having a few short ones.

**COROLLAS.** The shape, color and spotting of the corollas have been considered of taxonomic significance. The shape varies from funnel-form-campanulate to rotate with the limb reflexed. The corolla is plicate, and is truncate with the exception of *P. Alkekengi* in which the lobes are separated by short sinuses. The shape of the corollas may be of taxonomic significance. Since the characteristic shape is attained for only a short time in the full sun, the application of this criterion is of limited value. Several species such as *P. lobata*, *P. Wrightii*, *P. hederæfolia* and *P. crassifolia* have corollas that are either rotate, or have a reflexed limb when fully open. Since the corollas are seldom fully open, the author has usually used a linear measurement for comparative purposes where such usage seemed desirable.

Color of the corolla has been used to help characterize *P. lobata*, which is our only species with a bluish, or violet, corolla. Otherwise the presence, and sometimes the color, of five spots on the limb of the yellowish corolla near its base has been found useful. The majority of the species either have distinct, dark spots present, or they have none that are noticeable in herbarium specimens. A few taxa such as *P. hederæfolia* var. *Fendleri* and some of the maritime varieties of *P. viscosa* have spots which are only a little darker than the rest of the corolla.

**STAMENS.** Size and color of the anthers are of taxonomic value. With a few exceptions, large anther size (measurements given in the keys) and thick filaments are correlated with our perennials. Small anther size and slender filaments are usually found in our annual species. In some taxa anther color is of significance. So many of the annual species have blue anthers that the yellow anthers of *P. missouriensis* attract attention. In others, such as *P. heterophylla* and *P. virginiana* var. *virginiana*, yellow or bluish tinged anthers seem to occur without much significance. However, *P. virginiana* var. *subglabrata* and var. *sonorae* may be dis-

tinguished by the bluish anthers of the former and the yellow anthers of the latter even when their other characteristics overlap.

A peculiarity of *P. crassifolia* and its var. *versicolor* is the presence of a few long jointed hairs on the filaments.

**FLOWERING CALYX.** The relative depth to which the calyx lobes are divided may be of value, as it is in helping to separate *P. angulata* var. *angulata* from var. *pendula*.

**PEDUNCLE.** The length of the peduncle, both flowering and fruiting, may be of taxonomic significance. In fruiting material of *P. ixocarpa* and *P. virginiana* var. *subglabrata*, some specimens of which may resemble each other, the very short fruiting peduncle of the former will serve to separate the two. Among the southwestern desert species, *P. hederacifolia* and its relatives may be separated from *P. crassifolia* and its relatives by the short flowering peduncle of the former. Although of lesser significance in the *P. angulata* complex, it may be used, in conjunction with the size of the fruiting calyx, to help separate *P. angulata* var. *angulata* from var. *pendula* and var. *lanceifolia*.

**FRUITING CALYX.** The calyx greatly enlarges with the maturing fruit, usually being much inflated around it. In some populations the size and shape seem to be constant, and characteristic enough to be taxonomically usable. In *P. pubescens* and its relatives there is present a distinctly five-angled fruiting calyx. A population in southern Arizona is proposed as a new species, easily recognized by its unusually broad, sharply-angled fruiting calyx. In the *P. angulata* series, *P. angulata* var. *angulata* has a larger fruiting calyx than either var. *pendula* or var. *lanceifolia*.

In other populations the size and shape of the fruiting calyx seem to be either quite variable, or the extremes occur sporadically. The present author believes that the large-calyx form described as *P. macrophysa* is a more or less sporadically occurring form of *P. virginiana* var. *subglabrata*, although it also may be found in intergrades with var. *sonorae* (*P. longifolia*). Specimens with large fruiting calyces also appear in *P. virginiana* var. *virginiana* and in some phases of *P. viscosa*.

The length of the lobes of the fruiting calyx was considered characteristic enough by Standley (l.c.) to call a new species *P. caudella*.

The writer has not found the indentation at the base of the

fruiting calyx to be of much taxonomic value. Considerable variation may occur on the same plant. Of course if the calyx is nearly filled by the berry, it will be little invaginated.

OTHER CHARACTERISTICS. The style has not been used to any extent. In *P. lobata* it is distinctively curved near the base and bent to one side. The more or less reniform, punctate to reticulate seeds are very similar in most of the species. Differences seen in preliminary study appear to be bridged by many intermediates when a large series is examined. The backs of the seed of *P. lobata* are rather crenate or rugose.

#### GENERIC RELATIONSHIPS

The genus *Physalis* is studied here in its more or less conventional conception, including those members of the *Solanaceae* having a funnelform or campanulate to rotate, or rotate-reflexed corolla, longitudinally dehiscing anthers, and a berry, or berry-like fruit, enclosed in an enlarged and usually inflated calyx. It excludes both *Margaranthus*, with its urceolate corollas and very *Physalis*-like fruiting calyces, and also *Chamaesaracha* with a corolla very similar to some species of *Physalis*, but with a fruit very closely invested by the enlarging calyx.

When not in flower, *Margaranthus* could hardly be distinguished from moderately small-fruited species of *Physalis*. The rather tightly investing fruiting calyx of *Chamaesaracha* can be matched, or is approached, in some specimens of certain species of *Physalis* such as *P. ixocarpa*. A peculiar situation is found in *Chamaesaracha* where *C. grandiflora*, originally described as *Physalis* by Hooker, and a related species, *C. nana*, have seeds very similar to the punctate or minutely reticulate seeds of *Physalis*, while the other species of the genus have rather strongly alveolate surfaces.

Possibly both genera should be included in *Physalis*. This would make *Physalis* an inclusive genus, similar in its concept to *Oenothera* as delimited by Munz and other conservative taxonomists. In that genus a number of subgenera, regarded as genera by some authors, are bound together by flower similarities despite their differently shaped fruits. In *Physalis*, under this broad concept, the distinctive fruiting calyx would hold together subgenera differing in corolla structure. In *Chamaesaracha* the dis-

tinctiveness of the fruiting calyx becomes progressively less evident. The difficulty here would be in finding a stopping place short of including the whole genus. The author prefers making a more intensive study of the problem before proceeding with such action.

Since there is the possibility of creating distinctive subgenera as outlined in the preceding paragraph, it seems preferable not to formally place the species here treated into subgenera or sections, but to defer this action until not only species of *Physalis* from other areas, but also related taxa can be studied.

#### TAXONOMY

**PHYSALIS** L., *Species Plantarum* 1: 182. 1735; *Alkekengi* Tourn. ex Hall, *Enum. Stirp. Helv.* 2: 508. 1742; *Herschellia* Bowdich, *Excurs. Mader.* 159. 1825. *Quincula* Raf. *Atl. Journ.* 145. 1832; *Alicabon* Raf., *Sylva Tellur.* 56. 1838; *Pentaphiltrum* Reichb., *Das Herbarienbuch* 121. 1841; *Boberella* Krause, in Sturm, *Fl. Deutschl.* ed. 2 (10): 54. 1903.

Plants annual or perennial with herbaceous stems, some having woody caudices, others with short to elongated rhizomes; leaves usually broadly ovate to linear, alternate or sometimes two at a node; vestiture various in kind and quantity, including short hairs, long jointed hairs, stipitate or sessile glands, or with hairs variously branched to stellate; corollas plicate, campanulate to rotate with the limb reflexed; corolla color usually some shade of yellow with, or without, five darker spots near the base of its limb, sometimes blue; flowers usually solitary in the axils of the leaves, sometimes on foreshortened axillary branches causing them to appear to be in axillary fascicles; calyx united, its lobes distinct for a little over one-half to about one-fourth of its length; calyx lobes ovate-deltoid to narrowly lanceolate, sometimes acuminate; calyx enlarging with, and usually inflated around, the maturing fruit; fruit a two-carpellate many- to few-seeded berry, sometimes rather dry; style more or less filiform, usually expanding somewhat at its summit into a slightly capitate, but sometimes nearly truncate, stigma; stamens five, their filaments attached near the base of the corolla tube; anthers ovate-oblong to linear-oblong, dehiscing by lateral slits, yellow or bluish in color; filaments varying from nearly as wide as the anthers, and sometimes clavate, to slender and filiform.

(To be continued)